POPULATION ECOLOGY OF SOME SCIURID SPECIES OF NORTHWESTERN MINNESOTA

A THESIS

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INTRODUCTION

A population may be defined as the number of individuals of a species present in a defined area at a given time. Statistical qualities of this group are fundamental tools of population ecology. Thus, the basic demography of a population is very important in understanding the total ecology of that species. Changes in abundance and distribution were probably the first population characteristics described by naturalists. Later, more detailed demographic parameters were added, which formalized the field of population ecology. Natality, mortality, dispersal and rate of growth are examples of population statistics that are important in this field today.

Presence of five species of Sciuridae on the campus of the University of Minnesota Forestry and Biological Station in northwestern Minnesota provided a unique opportunity for teaching and for a long-term investigation of certain aspects of mammalian population dynamics. Spermophilus tridecemlineatus, S. franklinii, Tamias striatus, Eutamias minimus, and Tamiasciurus hudsonicus, are diurnal, fairly conspicuous mammals, that are easily trapped and handled. Initial objectives of the project were to instruct students in field techniques of vertebrate ecology.

The yearly accumulation of trapping records created a data reservior which I used to investigate sciurid population ecology. Objectives were as follows:

1) to evaluate yearly fluctuations in population densities with reference to cycles and climatic variables.

2) to compute basic demographic parameters, such as sex ratios, life tables, and survival curves.
3) to examine interspecific relationships and possible competition in this sciurid community.

It is felt that these data and analyses will contribute to the knowledge of small mammal biology and, especially, population ecology of sciurids.

Geographic distribution maps for the five species of sciurids are given in Figure 1. Spermophilus tridecemlineatus, the thirteen-lined ground squirrel, is a species that inhabits the central United States, in particular the tall and short grass prairie regions. Its range in Minnesota includes the entire state except for the far northeast corner. S. franklinii, the Franklin's ground squirrel, has a similar distribution but is more limited to the Grest Plains states. Again, the northeast corner of Minnesota is not included in its range. Tamias striatus, the eastern chipmunk, is aptly named since its range covers the eastern deciduous biome. In Minnesota, it is not found in the southwestern corner of the state. Eutamias minimus, the least chipmunk, is found in the boreal forest and throughout the mountain forests of the western states. This species only covers the northern half of Minnesota and does not go much beyond the study area to the southwest. The red squirrel, Tamiasciurus hudsonicus, is also an inhabitant of the northern boreal forest and Rocky Mountain states, but is found through the mixed forest of the eastern United States. Its range covers the entire state of Minnesota. Thus, of the five sciurid species, only E. minimus could be considered at the limit of its range.

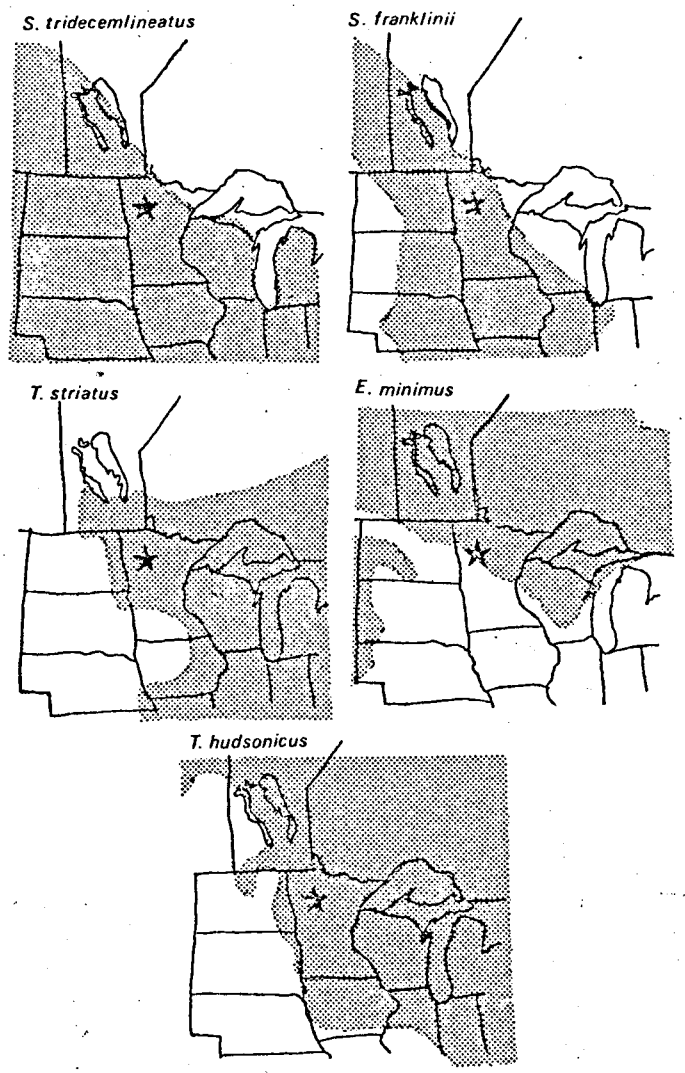


Figure 1. Local geographical distribution of the five sciurid species in the study. A star marks the location of the study area in Itasca State Park, Minnesota. From Hall and Kelson, 1959.

The study site, the campus of the University of Minnesota Forestry and Biological Station, is located within Itasca State Park in the SE ¼, Sec. 2, T. 43N, R. 35W, Clearwater County, Minnesota. Itasca State Park is well-known as being the headwaters of the Mississippi River and is geographically located at the junction of the three major North American biomes, coniferous forest, deciduous forest, and prairie. The vegetation of the park itself is a mixed coniferous-deciduous forest (Hansen et al., 1974).

Heterogeneous vegetation best describes the habitat at the Forestry and Biological Station. Numerous openings have been artificially created and maintained. Most notable is an athletic field of about 1.1 ha. This grassland habitat is surrounded by forest and functions as an "island" ecologically. Considerable "edge" between grassland and forest exists because of the disturbance by man, and adds to the heterogeneity.

Soil type for this area is termed a Nebish Variant-Unnamed association (U.S.D.A., 1975) and is described as "... well to somewhat excessively drained gently sloping to steep loamy and sand soils formed in sandy loam till and gravelly sand morainic deposits under forest vegetation."

METHODS

In 1953, students in a class in Vertebrate Ecology began the "Sciurid Project" under Dr. William Marshall. Similar data have been collected every summer through 1975. National live traps were set out on the 20 ha. campus for two to three weeks each summer. Animals captured were sexed, weighted, checked for reproductive status, and given permanent and temporary identification marks. Data were recorded on individual data sheets and also on key-sort cards after 1964. Ear tagging was used as a permanent marking system first, with toe clipping replacing it after 1956. Hair dye was applied in various patterns to enable observers to identify individual animals.

This data bank provided population samples through time. The first portion of analysis was to subject the number of adults of each species to cyclic testing. Data points were fitted to cosine functions of various periods by computer (Halberg et al., 1972). Auto correlation analysis was also performed with a BMD3D program (Dixon, 1973).

A second portion of analysis was aimed at determining if certain key climatic factors could be found which were responsible for the population fluctuations. The role of density dependence was also considered. First, population numbers were correlated against themselves and climatic variables using Pearson's correlation coefficients. Second, stepwise multiple regressions were performed on population numbers against climatic variables, and on weight averages against climatic variables.

Standardized computer programs from Biomedical Computer Programs, (BMD), were used (Dixon, 1973). Programs BMD3D, correlation with item deletion, BMD2R, stepwise regression, and BMD3R, multiple regression with case combination, were used on the Cyber 74 system at the University of Minnesota.

Weather data recorded at the Itasca Forestry and Biological Station were obtained from U.S. National Environmental Service reports. In addition, some climatic variables were taken from the work of Dr. Donald Baker in the University of Minnesota Soils Science Department and the St. Paul Campus Computing Center. These data were used as the independent variables in the regression analysis.

The 23 years of continuous record from one location is an attractive feature of these data. The largest drawback to a continuing class project is that there may be more variability between classes than between different years under a single researcher. This is a problem that must be analyzed closely before the data can be subjected to investigation. I have tried to look at various aspects of the project for large variations which might be a source of bias.

Figure 2. shows the trapping period for each year, 1953-1975. It is important to have each sampling period at the same time each year to avoid bias. For all aspects of the analysis except survivorship, only the data from the first summer sessions were used. This meant that four years could not be utilized since students only trapped during the second summer session in 1953, 1965, 1969, and 1971. It was felt that the later trapping period had biological

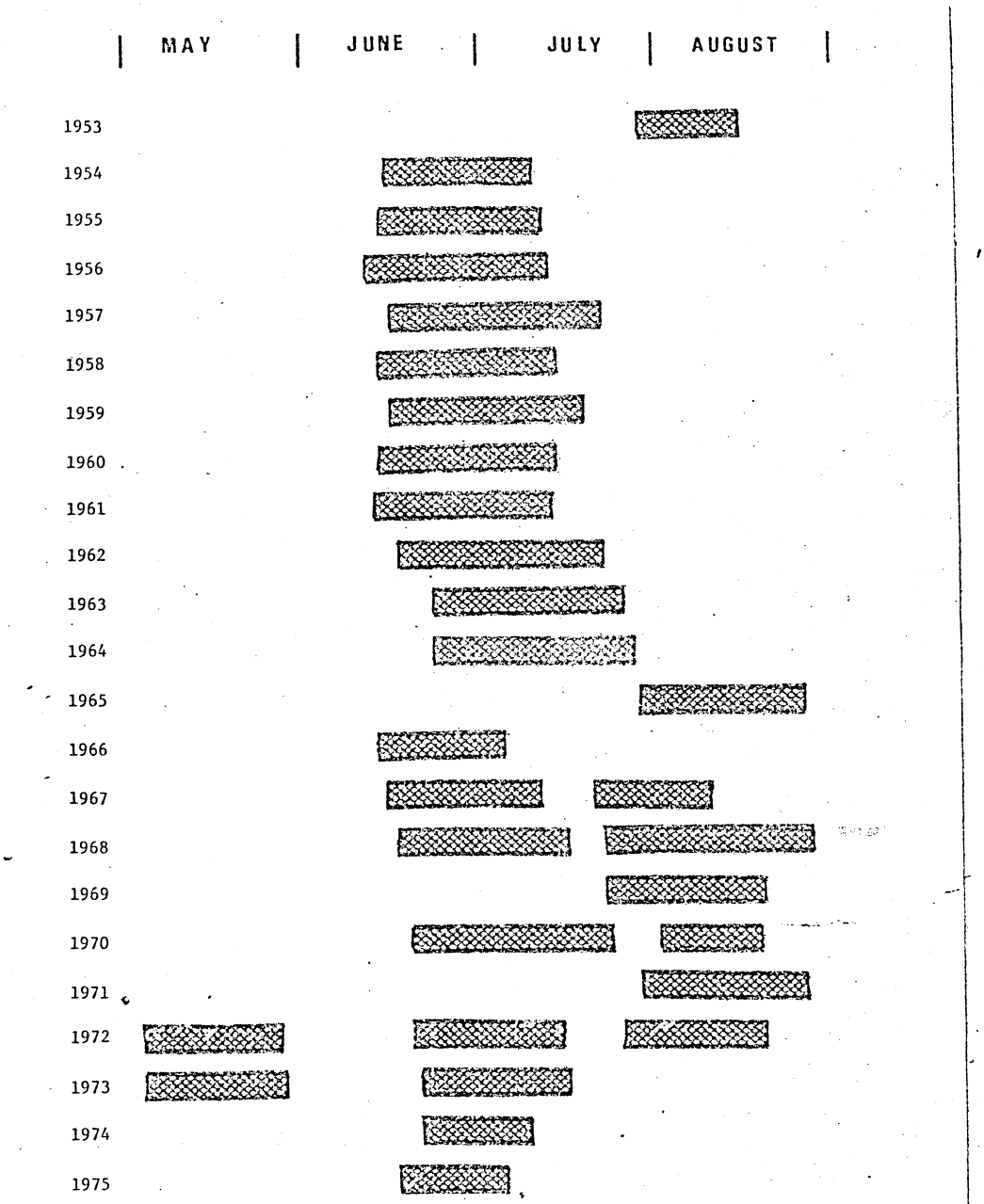


Figure 2. Trapping periods from 1953-1975 at the Itasca Forestry and Biological Station. Rectangles represent either spring, summer session I, or summer session II.

significance so as to bias the sampling. The adults may be in a non-reproductive status at this time, and the juveniles have grown to almost adult weight, making their age classification by weight more tenuous. Juveniles may also be dispersing more at this time, creating more immigration and emmigration in the study area, and possibly affecting the numbers captured. Data from 1954 were ommitted since use of grid maps did not begin until 1955. The first summer sessions had trapping periods that ranged from 16 to 36 days, generally running mid-June to mid-July. The average period was 29.4 days with a standard deviation of 5.5. This indicates that the trapping period has been consistent over the years in relation to any aspects of sciurid biology that might bias the samples.

The number of student trappers was not thought to be a significant source of variance in the study. Total class size has been about fifteen students. Since only a few people are needed to run a set of traps, the classes have always had sufficient numbers. A more serious limitation would be the number of traps used each year, since that could make a difference in the total productivity of the groups. The average number of traps has been 13.2 with a standard deviation of 3.2 for each species. This too, is consistent for the study, and should account for little bias in the samples. In trying to ascertain how much effort went into trapping each year, the number of traps used was multiplied by the days at least one animal was captured to obtain an estimate of effort expressed in trap-days. Figure 3. illustrates the effort in trap-days with the mean of 1026 trap-days indicated by the

Figure 3. Effort in trap-days per year from 1955-1975. Years 1965, 1969, and 1971 are excluded since no summer session I sampling was done.

TRAP-DAYS EFFORT
500
1000
1500
X
1955
1956
1957
1958
1959
1960
1961
1962
1963
1964
1966
1967
1968
1970
1972
1973
1974
1975
YEAR

dashed horizontal line. The standard deviation is 171 trap-days. Effort figures are sums of each of the efforts expended for the five species each year. It is assumed that all the traps allotted to each species group were set out on each trap day and that they were left out for the same length of time. It is highly improbable that such assumptions are met completely, but the information needed to clarify the situation was not recorded in each year's report. Despite this, the computed effort in trap-days is very consistent through the study.

Also of concern is whether the same area was trapped each year. Figure 4. shows the grid system utilized for recording location data. The grid code indicates the number of years at least one individual sciurid was captured. Each grid square represents about 0.09 ha. Of course the data only represent captures. One would rather know the area in which traps were set regardless of their success. Unfortunately, this information was not included in the majority of class progress reports. On the average, 49 percent of the 176 grid squares were trapped each year. If one also remembers that the home range of each species is much larger than a single grid square (Forbes, 1964; Holm, 1966; Haggerty, 1968; Kemp and Keith, 1970), every square need not be trapped to effectively cover the Itasca Forestry and Biological Station grounds. A free-ranging sciurid could easily come in contact with a trap if only every other grid square contained a trap at some time each season.

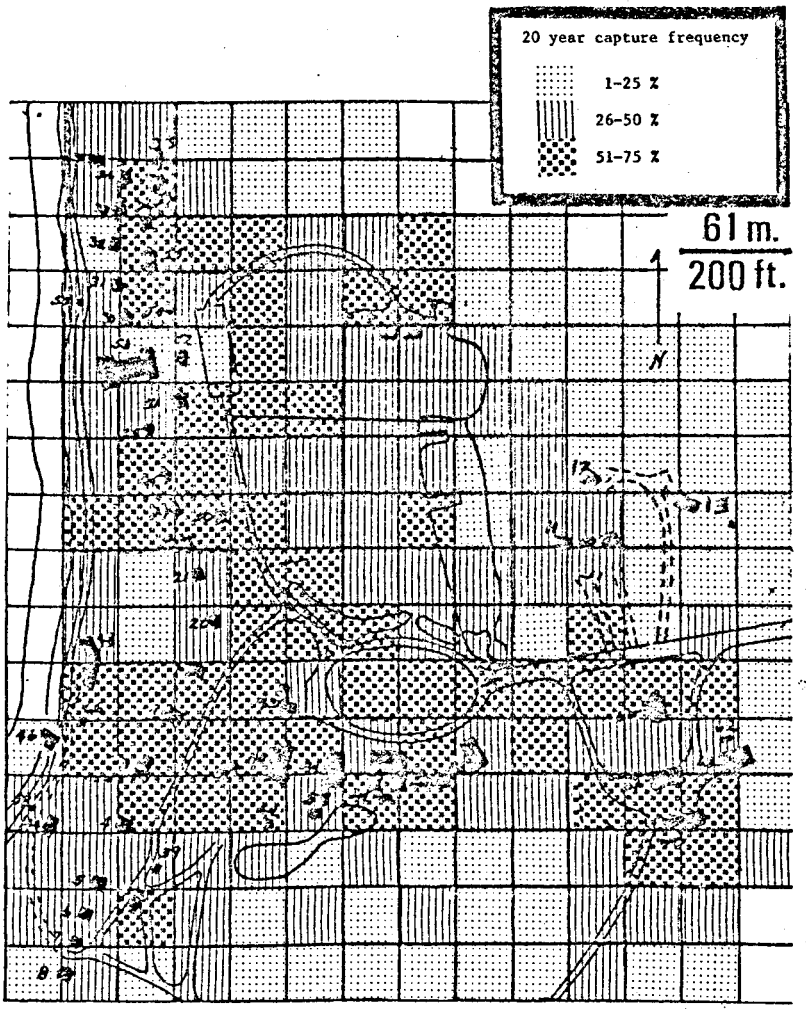


Figure 4. The Itasca Station grid map used since 1955. Darker pattern represents a greater % of the 20-year history (1956-1975) that at least one sciurid was captured in that grid.

RESULTS

During the study period, 1953-1975, the following numbers of sciurids were captured: 473 Spermophilus tridecemlineatus, 236 S. franklinii, 413 Tamias striatus, 163 Eutamias minimus, and 387 Tamiasciurus hudsonicus. The number of adults trapped each year is given in Figures 5. through 9.

Since the S. franklinii numbers subjectively appeared to be cyclic, on about a ten-year pattern, all populations were subjected to cycle analysis as outlined earlier. The results are tabulated for all five species in Table I. Significant levels of cyclic phenomena were found for four of five species by the cosine cyclic analysis, and three of five species had high "r" values with the auto correlation method. Length of cycle was consistent among both methods of analysis, especially in three species that were significant by both methods. Projected cosine curves were fit to the data for all five species and are given in Figure 10. The width of each cosine curve designates the 95% confidence limits ($\pm$1.96 S.D.).

Table II presents the average combined male/female ratio for these five species and ratios reported by other authors. The data are presented as percent of males in the sampled population. Most species have ratios that oscillate about 1:1. E. minimus demonstrates the greatest deviation from an equal sex ratio. This may be a result of the small sample size (163), and the fact that they are the smallest sciurid studies, hence presenting more of a problem to determine sex.

Figure 5. Number of adults trapped each year from 1955-1975 for Spermophilus tridecemlineatus. Unshaded rectangles represent samples from summer session II.

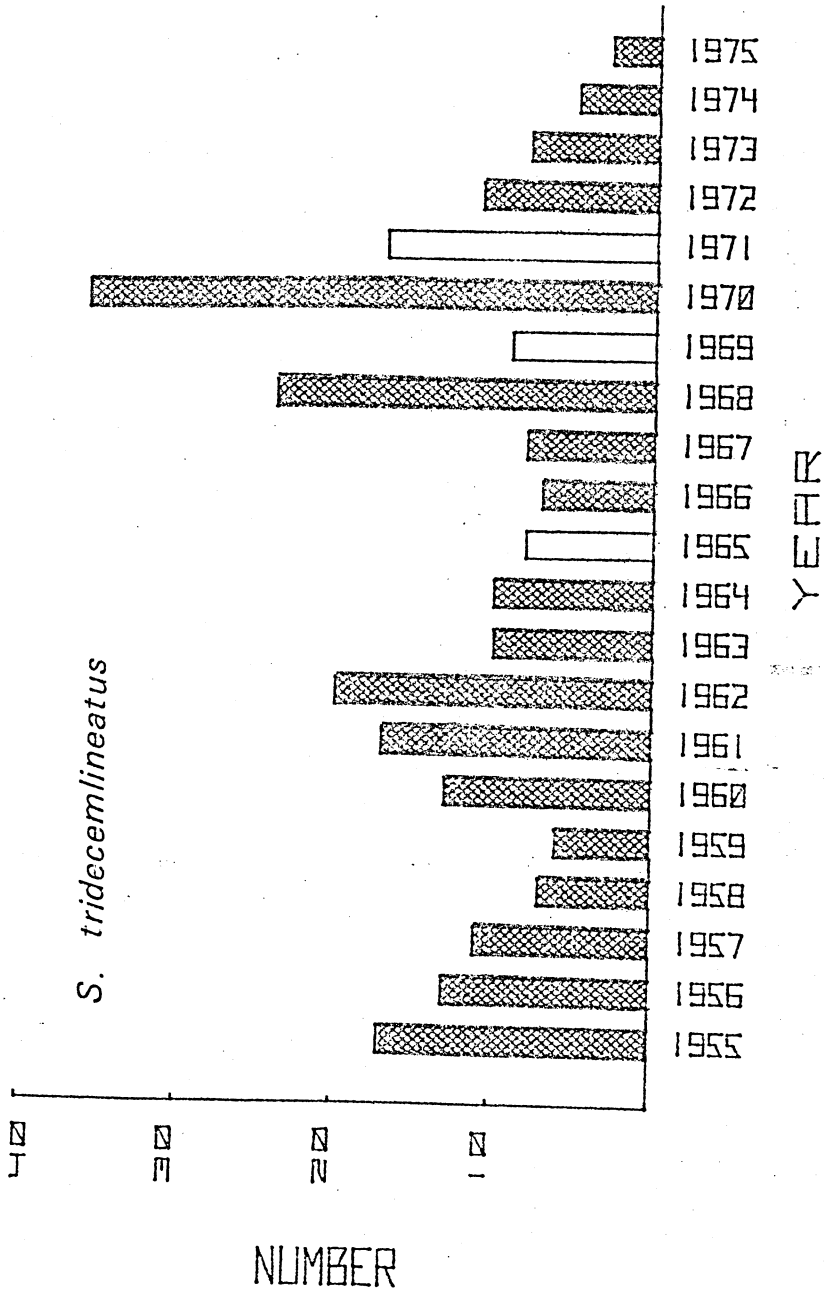

S. tridecemlineatus
1975
1974
1973
1972
1971
1970
1969
1968
1967
1966
1965
1964
1963
1962
1961
1960
1959
1958
1957
1956
1955
YEAR
NUMBER

Figure 6. Number of adults trapped each year from 1955-1975 for Spermophilus franklinii. Unshaded rectangles represent samples from summer session II.

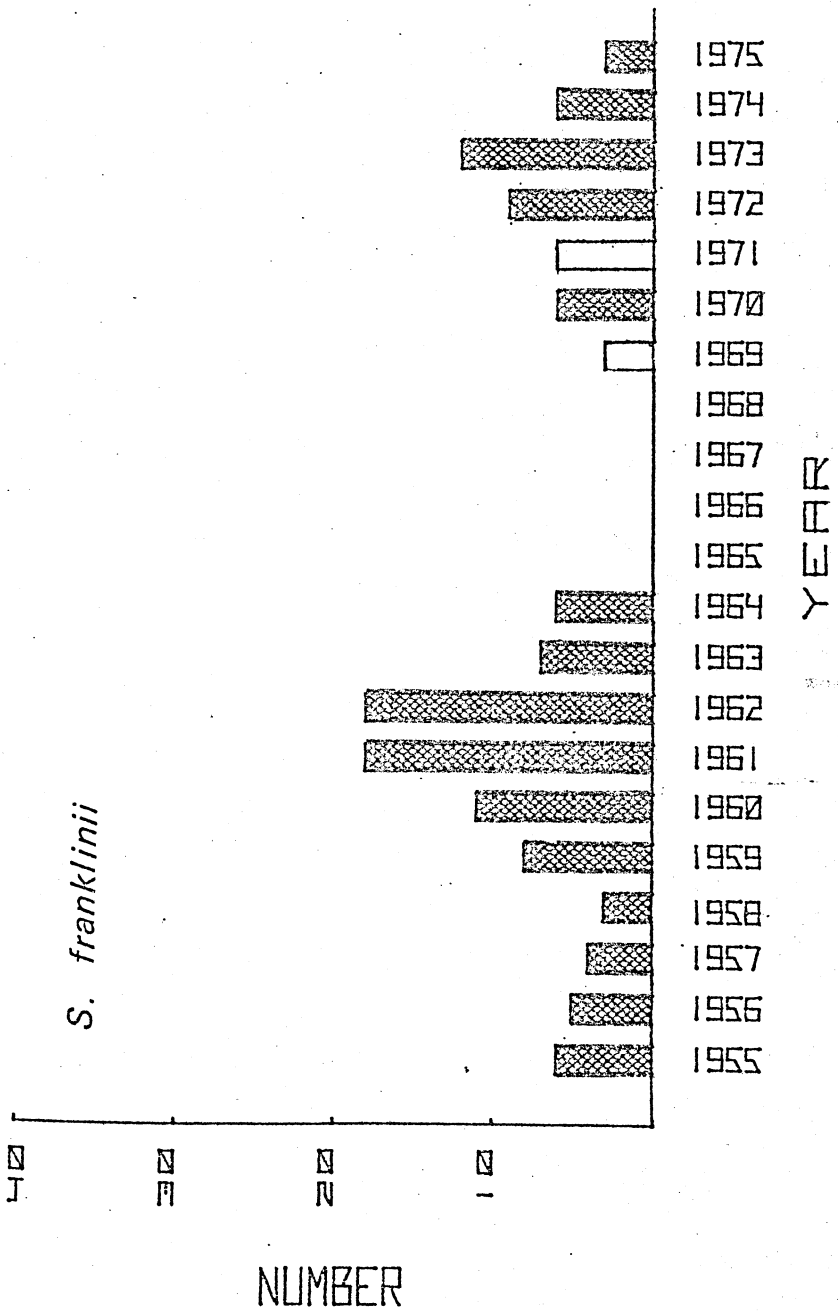

1975
1974
1973
1972
1971
1970
1969
1968
1967
1966
1965
1964
1963
1962
1961
1960
1959
1958
1957
1956
1955
YEAR
S. franklinii
NUMBER

Figure 7. Number of adults trapped each year from 1955-1975 for Tamias striatus. Unshaded rectangles represent samples from summer session II.

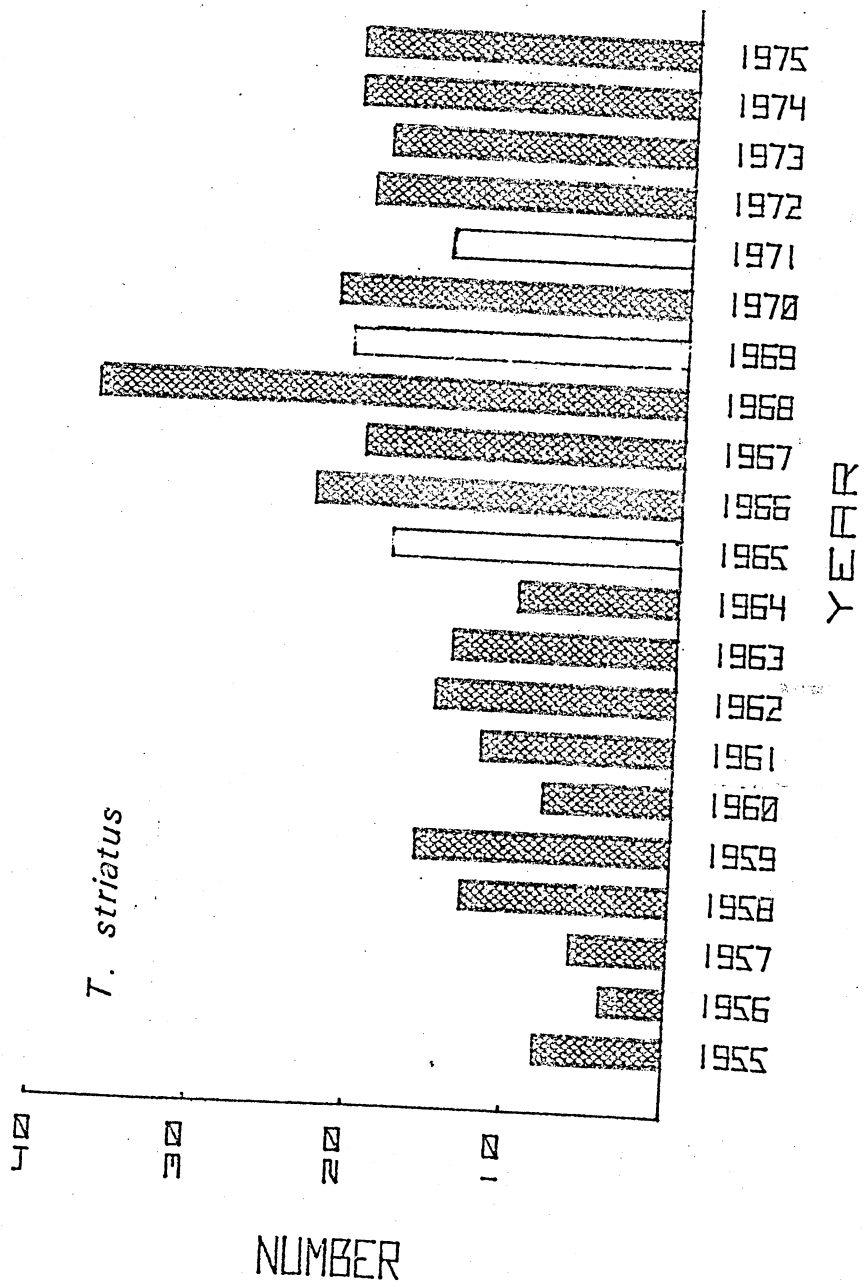

1975
1974
1973
1972
1971
1970
1969
1968
1967
1966
1965
1964
1963
1962
1961
1960
1959
1958
1957
1956
1955
YEAR
T. striatus
NUMBER

Figure 8. Number of adults trapped each year from 1955-1975 for Eutamias minimus. Unshaded rectangles represent samples from summer session II.

E. minimus
NUMBER
0
20
40
YEAR
1955
1956
1957
1958
1959
1960
1961
1962
1963
1964
1965
1966
1967
1968
1969
1970
1971
1972
1973
1974
1975

Figure 9. Number of adults trapped each year from 1955-1975 for Tamiasciurus hudsonicus. Unshaded rectangles represent samples from summer session II.

T. hudsonicus
NUMBER
0
20
40
YEAR
1955
1956
1957
1958
1959
1960
1961
1962
1963
1964
1965
1966
1967
1968
1969
1970
1971
1972
1973
1974
1975

Table I. Cycle analysis results from cosine function and auto correlation methods. Percent rhythm is the variability in the data that is accounted for by the cosine function. r^2 value is the similar measure for the auto correlation method.

Species	Cosine Analysis		Auto Correlation	
	Cycle Length years	% Rhythm	Cycle Length years	r^2
Spermophilus tridecemlineatus	8	45	8	.46
Spermophilus franklinii	10	69	11	.81
Tamias striatus	8	21	9	.19
Eutamias minimus	7	32	5	.19
Tamiasciurus hudsonicus	11	53	11	.59

Figure 10. Cyclic analysis by the cosine function for five sciurid species. Outside boundaries of each curve represent the 95% confidence limits. The horizontal line at the beginning of each curve represents the zero baseline for that population.

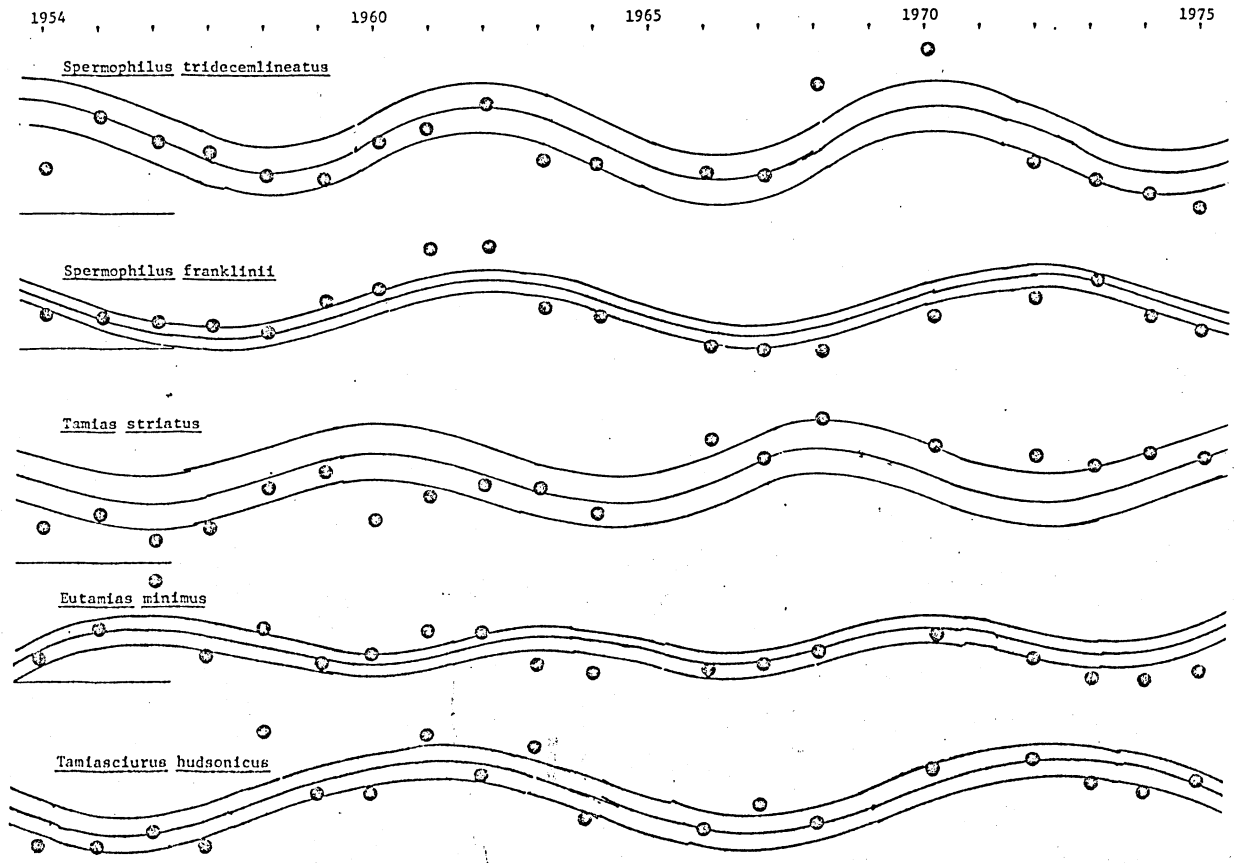

1954
1960
1965
1970
1975
Spermophilus tridecemlineatus
Spermophilus franklinii
Tamias striatus
Eutamias minimus
Tamiasciurus hudsonicus

Table II. Sex ratios of five sciurid species expressed as percent males in the population. Figures in parenthesis are sample sizes. Asterisks mark data from this study.

Species	Male % of population adult	juvenile	Source
Spermophilus tridecem-lineatus	35 (247)++	51 (196)	*
	31 (114)++	52 (290)	McCarley 1966
	38 (60)	51 (172)	Rongstad 1965
Spermophilus franklinii	43 (129)	47 (87)	*
	51 (47)	-	Iverson and Turner 1972
	41 (69)	50 (30)	Murie 1973
Tamias striatus	41 (294)++	63 (207)++	*
	57 (1218)++	52 (1500)	Tyron and Snyder 1973
	41 (56)	59 (22)	Pidduck and Falls 1973
Eutamias minimus	35 (93)++	70 (94)+	*
	58 (76)	-	Forbes 1966
	53 (195)	-	Sheppard 1968
Tamiasciurus hudsonicus	50 (324)	61 (122)+	*
	52	52	Kemp and Keith 1970
	53	52	Davis and Sealander 1971

+ significance at 95% level

++ significance at 99% level

The life tables of all five species were computed from the period 1953-1975. Tables III-VII give customary entries for the yearly age classes. In addition, Figures 11 through 15 plot the $\log_{10}$ of the survivors against their age in years. Each species is divided into cohorts of males and females. Diagonal lines (type II, Deevey, 1947) are indicative of age independent survival. Basically, all five species demonstrated such curves. This is seen in Figure 16. where males and females are combined and all five species are plotted together.

The life expectancy (e_x) for each sex was plotted against the yearly age classes for each species in Figure 17. Higher mortality for juveniles and old individuals is indicated by the convex curves. Species with small sample sizes deviate most from this pattern.

Average adult weight of each of the five species was computed for each of the years trapping in addition to an overall 22-year average. These are plotted in Figure 18. with time as the abscissa. $\pm$ 1.96 standard deviations are illustrated about each overall mean. The clear separation by weight averages is striking. There is no overlap between the 95% confidence limits of each overall average.

The results of the stepwise regressions are in Tables VIII, IX, and X. Sixteen independent variables are given in Table VIII, the first fifteen (#17-31) are climatic variables: the last one (#32) is a population variable. These were used for both of the stepwise regressions. The first regression used the total number of adults for the season as a dependent variable. Table IX gives the r^2 value for all 15 regressions. Each species is subdivided

Table III. Life table for Spermophilus tridecemlineatus from data from 1954-1975.

x age class in years	x' age as % dev. from mean length of life.	d_x no. dying in age interval of 1000 born	l_x no. surviving at start of age interval	$1000q_x$ mortality rate /1000 alive at start of interval	e_x expectation of life in years
MALES AND FEMALES				Mean length of life in	1.02 years
0-1	-100.0	712	1000	712.	1.02
1-2	- 2.3	164	288	569.	1.32
2-3	+ 95.3	64	124	516.	1.40
3-4	+193.0	24	60	400.	1.37
4-5	+290.6	20	36	556.	0.72
5-6	+388.3	16	16	1000.	0.50
MALES				Mean length of life	0.94 years
0-1	-100.0	748	1000	748.	0.94
1-2	+ 6.4	150	252	595.	1.25
2-3	+112.8	55	102	539.	1.34
3-4	+219.1	16	47	340.	1.33
4-5	+325.5	23	31	742.	0.76
5-6	+431.9	8	8	1000.	0.50
FEMALES				Mean length of life	1.11 years
0-1	-100.0	675	1000	675.	1.11
1-2	- 9.8	179	325	551.	1.37
2-3	+ 80.3	73	146	500.	1.45
3-4	+170.5	32	73	438.	1.39
4-5	+260.7	17	41	415.	1.09
5-6	+350.9	24	24	1000.	0.50

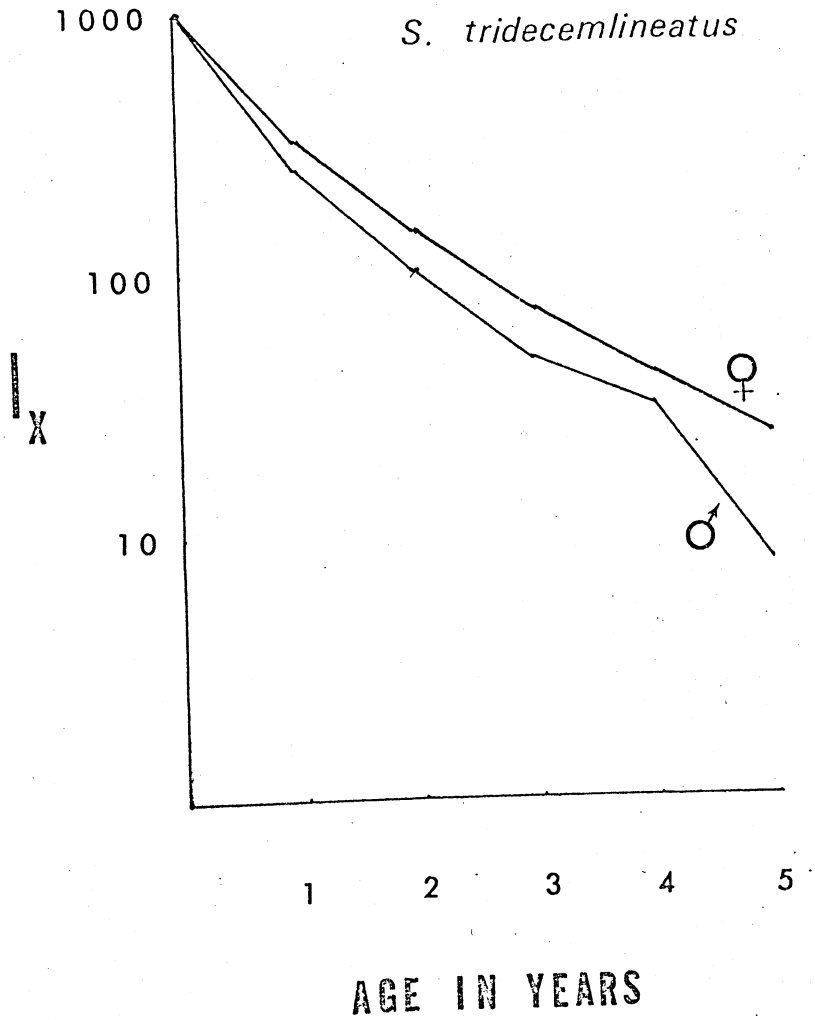


Figure 11. Survival curve for Spermophilus tridecemlineatus. Starting base of 1000 animals is calculated from a cumulative cohort of males and females from 1954-1970.

Table IV. Life table for Spermophilus franklinii from data from 1954-1975.

x age class in years	x' age as % dev. from mean length of life	d_x no. dying in age interval of 1000 born	l_x no. surviving at start of age interval	$1000q_x$ mortality rate /1000 alive at start of interval	e_x expectation of life in years
MALES AND FEMALES				Mean length of life in 0.74 years	
0-1	-100.0	868	1000	868.	0.74
1-2	+ 34.8	74	132	560.	1.31
2-3	+169.6	25	58	431.	1.34
3-4	+304.4	25	33	758.	0.98
4-5	+439.3	0	8	000.	1.00
5-6	+574.1	8	8	1000.	0.50
MALES				Mean length of life 0.65 years	
0-1	-100.0	873	1000	873.	0.65
1-2	+ 55.0	109	127	858.	0.64
2-3	+210.1	18	18	1000.	0.50
4-5					
5-6					
FEMALES				Mean length of life 0.82 years	
0-1	-100.0	864	1000	864.	0.82
1-2	+ 22.2	45	136	330.	1.84
2-3	+144.4	30	91	330.	1.50
3-4	+266.7	46	61	754.	0.99
4-5	+389.0	0	15	000.	1.50
5-6	+511.2	15	15	1000.	0.50

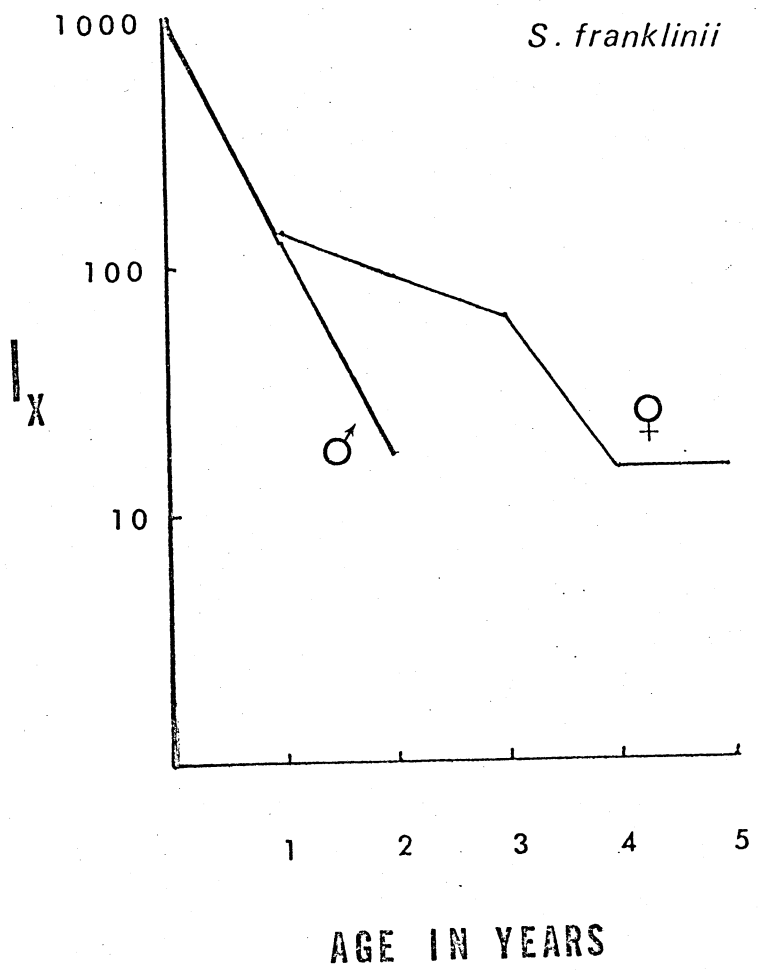


Figure 12. Survival curve for Spermophilus franklinii. Starting base of 1000 animals is calculated from a cumulative cohort of males and females from 1954-1970.

Table V. Life table for Tamias striatus from data from 1954-1975.

MALES AND FEMALES — Mean length of life 1.14 years

x	x'	d_x	l_x	$1000q_x$	e_x
age class in years	age as % dev. from mean length of life.	no. dying in age interval of 1000 born	no. surviving at start of age interval	mortality rate /1000 alive at start of interval	expectation of life in years
0-1	-100.0	618	1000	618.	1.14
1-2	- 12.4	237	382	620.	1.18
2-3	+ 75.3	69	145	476.	1.29
3-4	+162.9	38	76	500.	1.01
4-5	+250.6	38	38	1000.	0.50

MALES — Mean length of life 1.09 years

0-1	-100.0	658	1000	658.	1.09
1-2	- 7.8	199	342	582.	1.21
2-3	+ 84.3	72	143	503.	1.20
3-4	+176.5	42	71	592.	0.91
4-5	+268.7	29	29	1000.	0.50

FEMALES — Mean length of life 1.21 years

0-1	-100.0	574	1000	574.	1.21
1-2	- 21.3	278	426	652.	1.15
2-3	+ 57.4	66	148	446.	1.39
3-4	+136.0	33	82	402.	1.10
4-5	+214.7	49	49	1000.	0.50

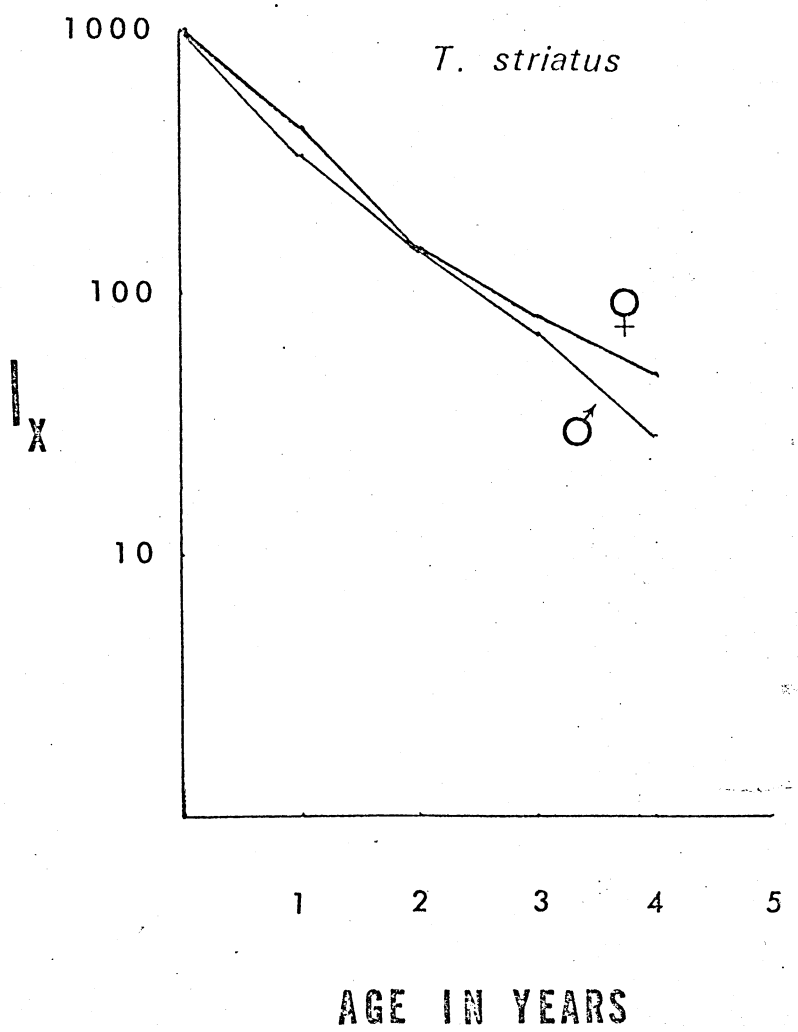


Figure 13. Survival curve for Tamias striatus. Starting base of 1000 animals is calculated from a cumulative cohort of males and females from 1954-1970.

Table VI. Life table for Eutamias minimus from data from 1954-1975.

x	x'	d_x	l_x	$1000q_x$	e_x
	MALES AND FEMALES			Mean length of life 0.66 years	
age class in years	age as % dev. from mean length of life	no. dying in age interval of 1000 born	no. surviving at start of age interval	mortality rate /1000 alive at start of interval	expectation of life in years
0-1	-100.0	902	1000	902.	0.66
1-2	+ 51.7	49	98	500.	1.12
2-3	+203.5	37	49	755.	0.74
3-4	+355.2	12	12	1000.	0.50
	MALES			Mean length of life 0.59 years	
0-1	-100.0	966	1000	966.	0.59
1-2	+ 70.9	0	34	000.	2.00
2-3	+242.9	17	34	500.	1.00
3-4	+412.8	17	17	1000.	0.50
	FEMALES			Mean length of life 0.85 years	
0-1	-100.0	739	1000	739.	0.85
1-2	+ 17.9	174	261	667.	0.83
2-3	+135.8	87	87	1000.	0.50
3-4					

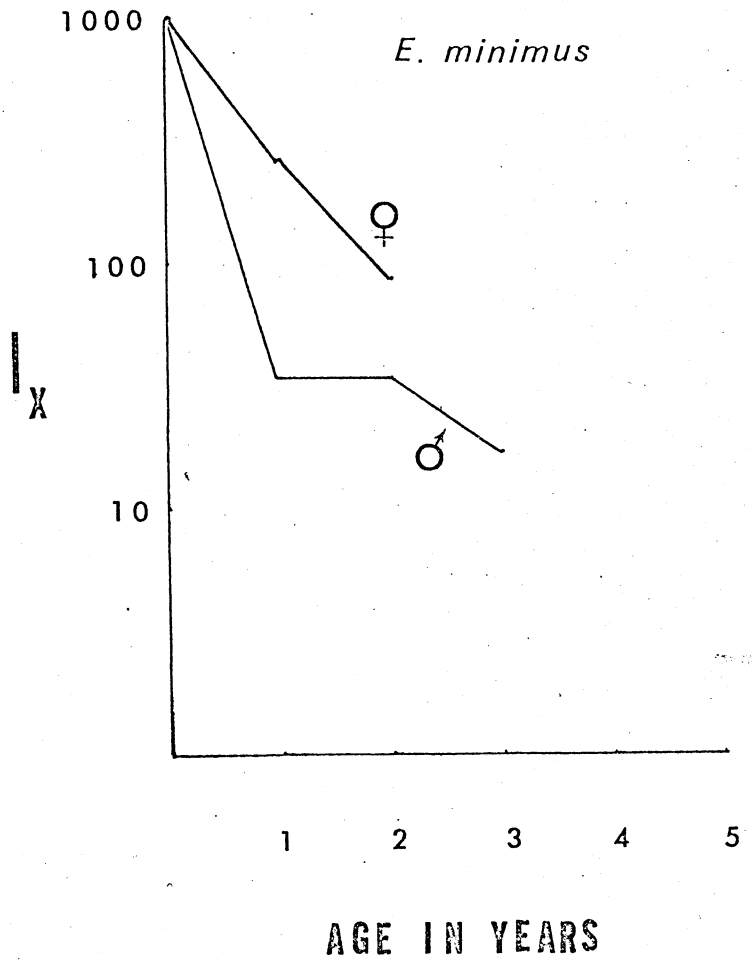


Figure 14. Survival curve for Eutamias minimus. Starting base of 1000 animals is calculated from a cumulative cohort of males and females from 1954-1970.

Table VII. Life table for Tamiasciurus hudsonicus from data from 1954-1975.

x	x'	d_x	l_x	$1000q_x$	e_x
	MALES AND FEMALES			Mean length of life 0.81 years	
age class in years	age as % dev. from mean length of life	no. dying in age interval of 1000 born	no. surviving at start of age interval	mortality rate /1000 alive at start of interval	expectation life in years
0-1	-100.0	835	1000	835.	0.81
1-2	+ 23.3	78	165	473.	1.38
2-3	+146.6	38	87	437.	1.18
3-4	+269.9	39	49	796.	0.70
4-5	+393.2	10	10	1000.	0.50
	MALES			Mean length of life 0.66 years	
0-1	-100.0	905	1000	905.	0.66
1-2	- 51.7	47	95	495.	1.17
2-3	+203.5	32	48	667.	0.83
3-4	+355.2	16	16	1000.	0.50
4-5					
	FEMALES			Mean length of life 1.05 years	
0-1	-100.0	725	1000	725.	1.05
1-2	- 4.8	125	275	455.	1.50
2-3	+ 90.5	50	150	333.	1.33
3-4	+185.7	75	100	750.	0.75
4-5	+281.0	25	25	1000.	0.50

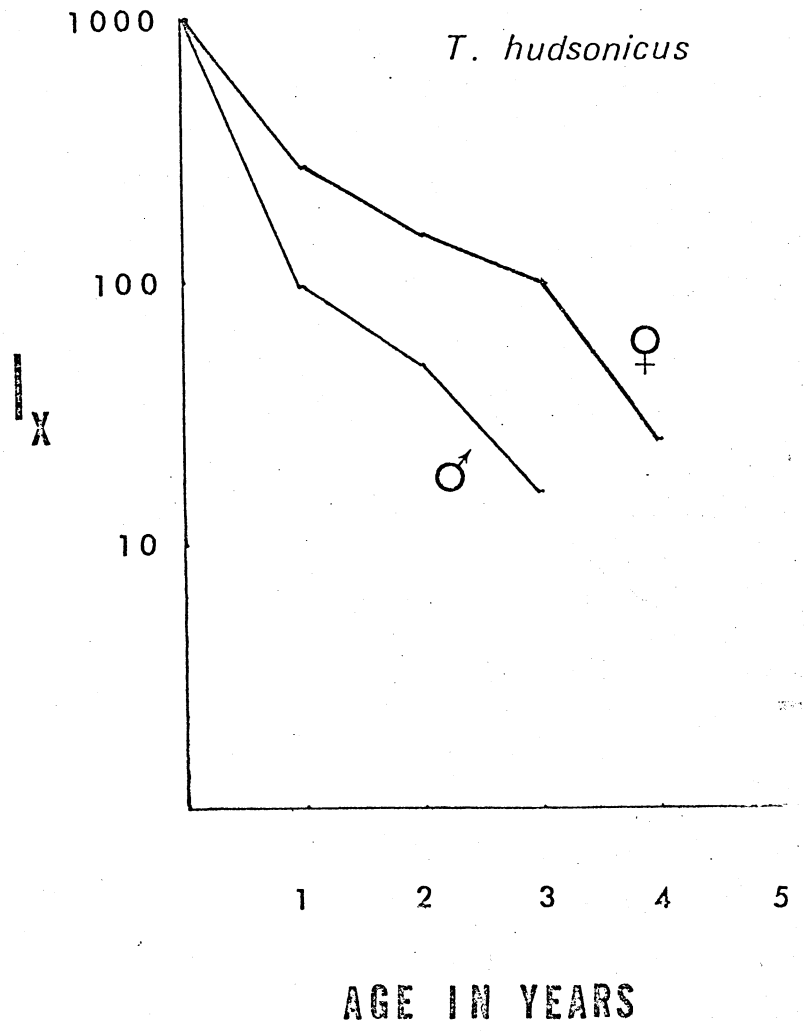


Figure 15. Survival curve for Tamiasciurus hudsonicus. Starting base of 1000 animals is calculated from a cumulative cohort of males and females from 1954-1970.

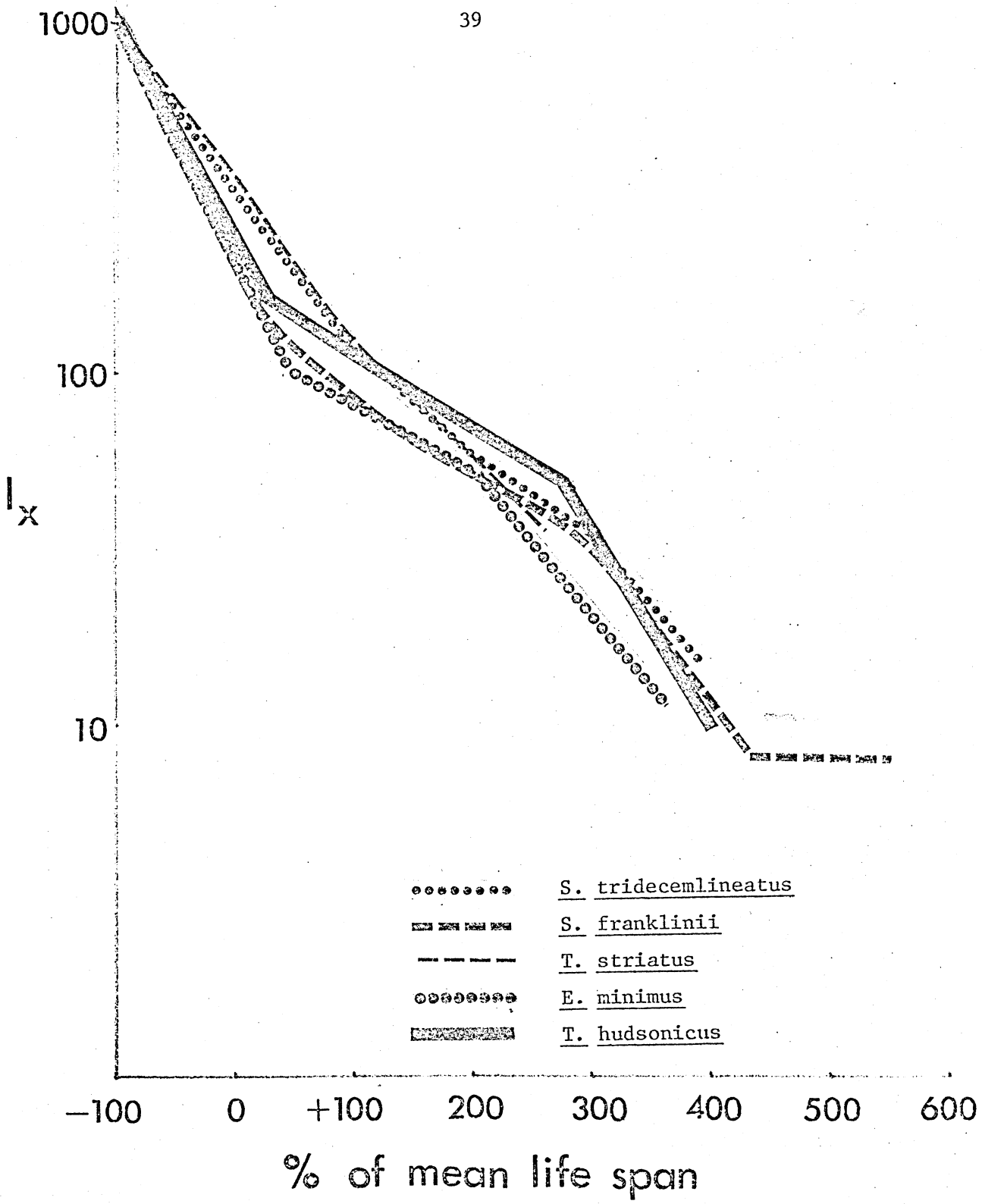


Figure 16. Comparison of survivorship of the five sciurid species. The abscissa is the % deviation from the mean length of life. Each species' curve is for males and females combined.

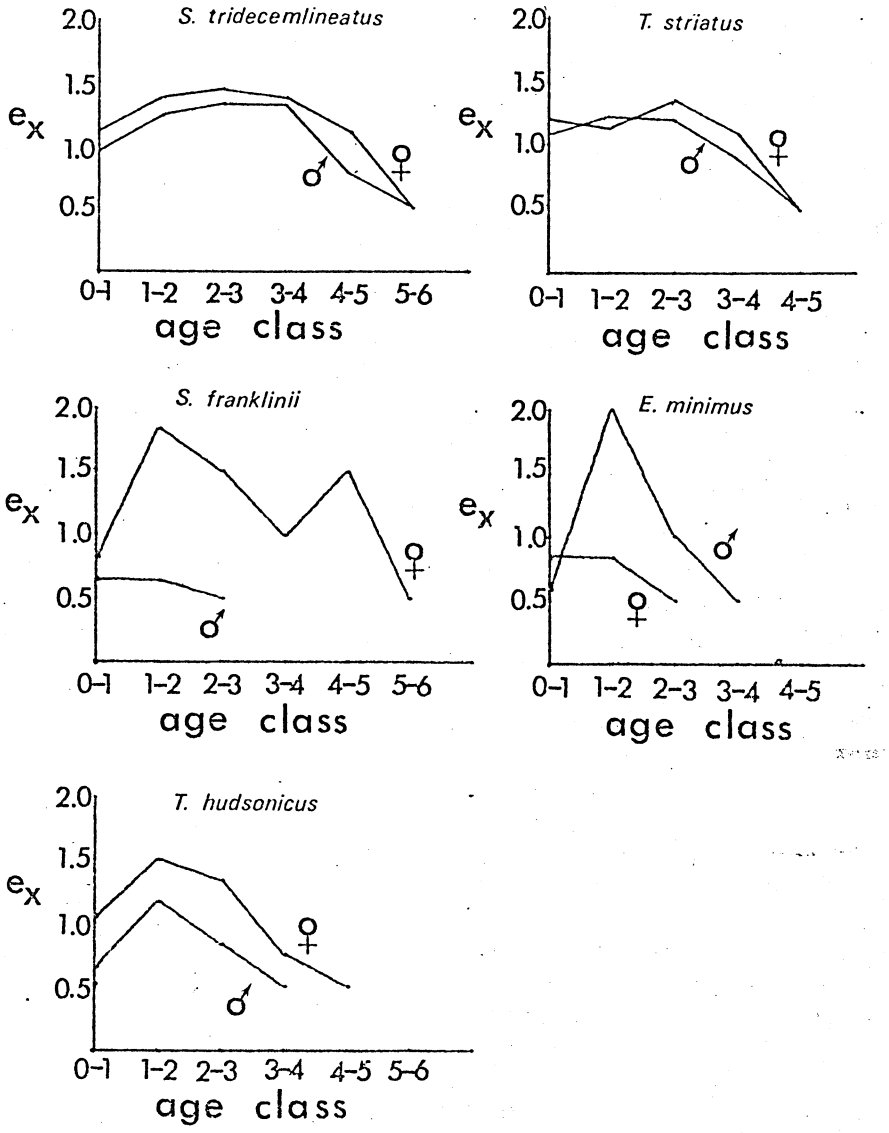


Figure 17. Life expectancy (e_x) of each yearly age class of five sciurid species at Itasca 1954-1970.

Figure 18. Average adult weight for each sciurid species for the years 1954-1975. Overall weight averages are represented by a horizontal line and $\pm$ 1.96 standard deviation by a rectangle. (95% confidence limits).

WEIGHT IN GRAMS
0
50
100
150
200
250
300
350
400
S. franklinii
T. hudsonicus
S. tridecemlineatus
T. striatus
E. minimus
1954
1955
1956
1957
1958
1959
1960
1961
1962
1963
1964
1965
1966
1967
1968
1969
1970
1971
1972
1973
1974
1975
YEAR

Table VIII. Independent variable code.

17	last frost day less than 32° F.; days from 1 May to last frost.
18	number of frost-free days, greater than 32° F.
19	last frost day less than 28° F.; days from 1 May to last frost.
20	number of frost-free dyas greater than 28° F.
21	summer mean temperature (June-August).
22	total precipitation for growing season (April-September).
23	corn growing degree days, 50 - 85° F. (May-October).
24	number of days greater than 90° F.
25	winter mean temperature (December-February).
26	heating degree days, 65° F. base.
27	number of continuous days where temp. max. was less than 32° F.
28	number of continuous days where temp. max. was less than 0° F.
29	cooling degree days, 75° F. base.
30	winter index, winter mean temp. times total winter precip. (November-February).
31	spring precipitation (April-June).
32	adult intraspecific population from the previous year.

Table IX. Stepwise regression results with number of adults each season as the dependent variable and 16 independent variables (listed in Table VIII).

Dependent Variable by Species & Sex Class	Independent Variables Contributing 0.1 r^2 (in decreasing values)				r^2
Spermophilus tridecemlineatus					
males	24	21*	29		.7433
females	27*	20	22*		.6393
total	27*	29*			.5768
Spermophilus franklinii					
males	23*	21*			.5460
females	23*	29	18		.4952
total	23*	21			.4864
Tamias striatus					
males	28*	21*			.5741
females	28*				.6178
total	28*	19			.6543
Eutamias minimus					
males	27	28*	18*		.6104
females	23*	28	24	18*	.7319
total	23*	28	27*	18	.7124
Tamiasciurus hudsonicus					
males	22*	30*			.6854
females	30*	22*			.4881
total	30*	22*			.6819

* significance at $F_{.95}$ level.

Table X. Results of stepwise regression with average summer weight as dependent variable and 16 independent variables (listed in Table VIII).

Dependent Variable by Species & Sex Class	Independent Variables Contributing 0.1 r^2 (in decreasing values)				r^2
Spermophilus tridecemlineatus					
males	31*	29	25		.6288
females	19	26			.3711
total	19	31			.3676
Spermophilus franklinii					
males	28*	30*	21*		.8179
females	30*	32*	22*		.7786
total	30*	28*	32*	22*	.8793
Tamias striatus					
males	30	17	24		.5245
females	22*	21*	32*		.6605
total	21	22	32		.5253
Eutamias minimus					
males	29*	30	19	24	.8609
females	30*	21*			.8540
total	30*	29*			.8632
Tamiasciurus hudsonicus					
males	23*	31	30		.5605
females	17*	30	24		.5139
total	17*	30	23		.5138

* significant variables at $F_{.95}$ level.

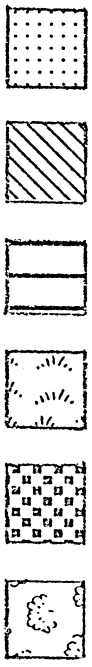
into adult males, adult females, and total adults. In each case, the independent variables are listed that contributed at least 0.1 r^2 value. They are in decreasing order of importance with significant variables (at a $F_{.95}$ level) marked by an asterisk. Very few independent variables are found consistently within or between species. Cumulative r^2 values are quite varied and most account for more than 50% of the observed variation in the dependent variable.

The results of the second regression, using the average adult weight for the season as the dependent variable, are given in Table X. These data are reported in the same manner as Table IX. Different independent variables were generated in this regression, but their consistency within and between species was not improved. Levels of r^2 were slightly more variable.

A habitat map was generated by placing each grid square into one of six habitat types. These vegetation zones were based mainly on physiognomic characteristics and dominant tree species. The resultant map is given in Figure 19. and shows the habitat heterogeneity of the station. Only those grid squares that had a history of a sciurid capture were included in the vegetation map. Although the habitat survey was done in 1975, it was quite similar to a vegetation map completed in 1955. This is not to say that the plant species composition has not changed in 23 years, but only that the physiognomic categories outlined have stayed fairly constant.

When the trapping locations of a species are tallied for the last 20 years, certain areas are found to be more successful

Figure 19. Vegetation zones of the Itasca Forestry and Biological Station.



mixed deciduous-coniferous woods

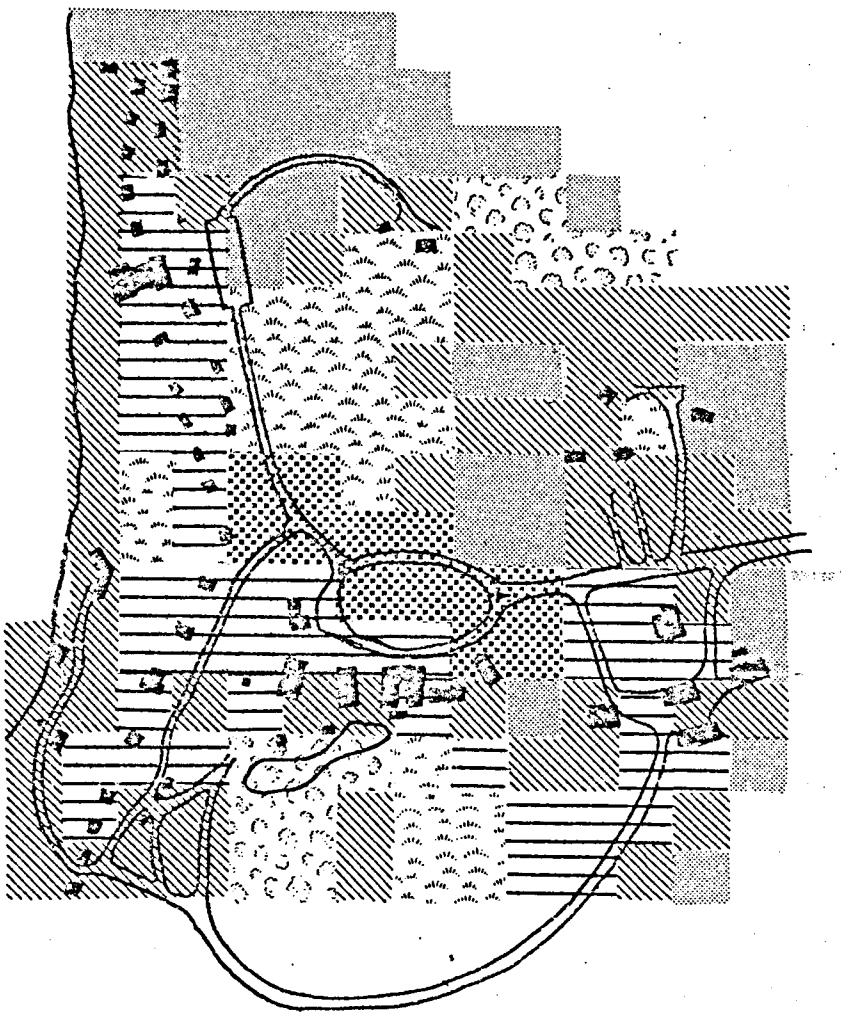
edge between woods and open areas

openings with occasional trees and a grass understory

grassy areas with no trees or shrubs

spruce and fir areas

deciduous woods



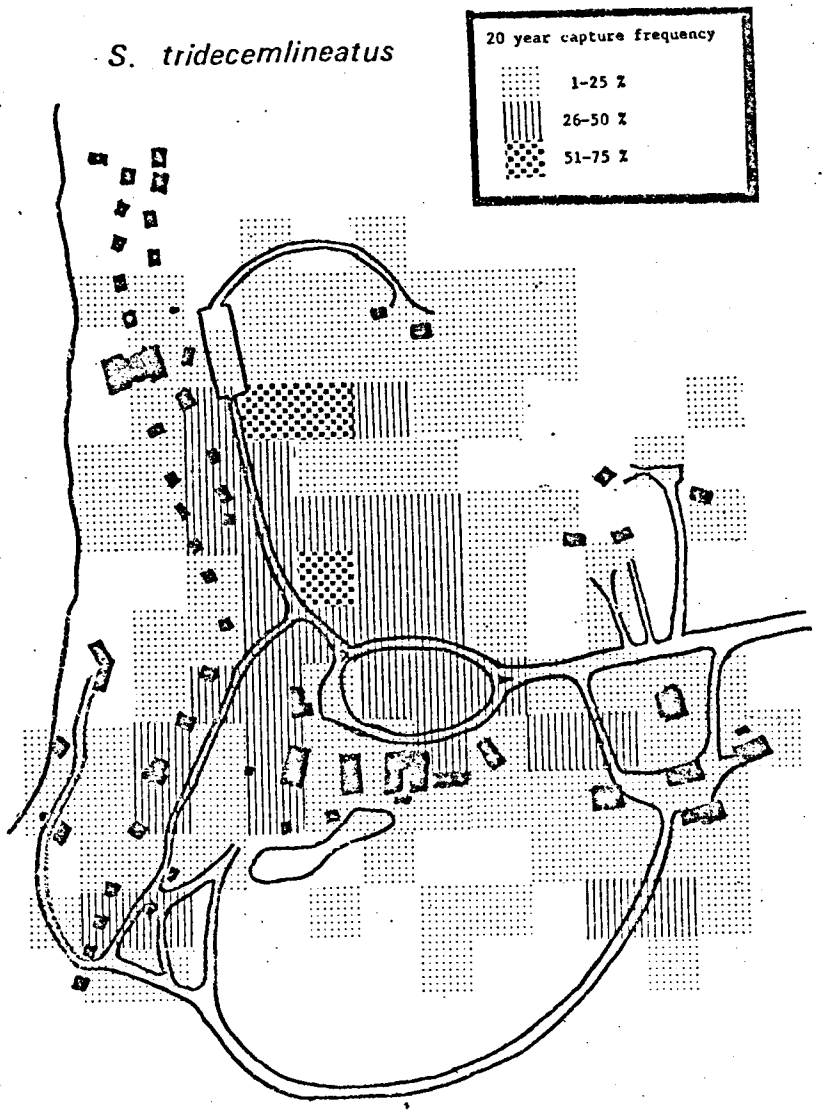


Figure 20. Frequency of at least one capture each year from 1956-1975 for Spermophilus tridecemlineatus.

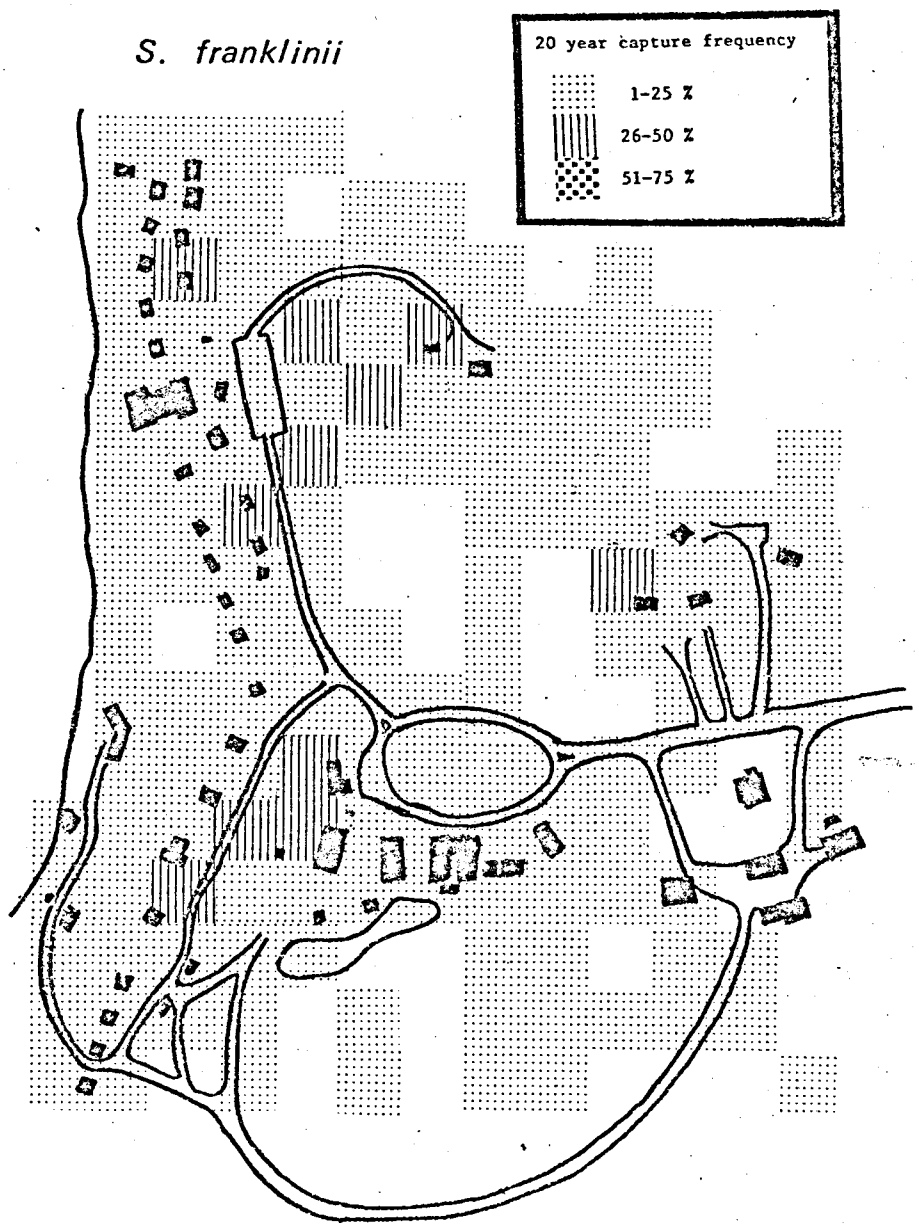


Figure 21. Frequency of at least on capture each year from 1956-1975 for Spermophilus franklinii.

than others. This may be termed the preferred habitat of the species. Figures 20. through 24. outline the areas of high frequency of capture for each sciurid species. S. tridecemlineatus was trapped almost exclusively in the open mowed grass, especially the athletic field (Figure 20). S. franklinii, on the other hand, was not found as often in the open fields (Figure 21) but was captured along the edges of such grassy areas. This mixture is quite common as seen earlier in Figure 19.

Tamias striatus has a very similar habitat according to the trapping records (Figure 22). This species is found in a shrub understory, such as Corylus spp., using it both for food and protection.

Eutamias minimus trappings are not as numerous as the other species, therefore the habitat usage map may be less reliable, (Figure 23). There does appear to be an association with "edge" habitat around buildings.

Tamiasciurus hudsonicus shows a strong affinity to fir and spruce areas (Figure 24). This seems obvious since their food and shelter are mainly derived from these tree species. Few animals were captured in deciduous areas, or the open grassy habitat. A small spruce plantation was found to be a reliable trapping area for many years.

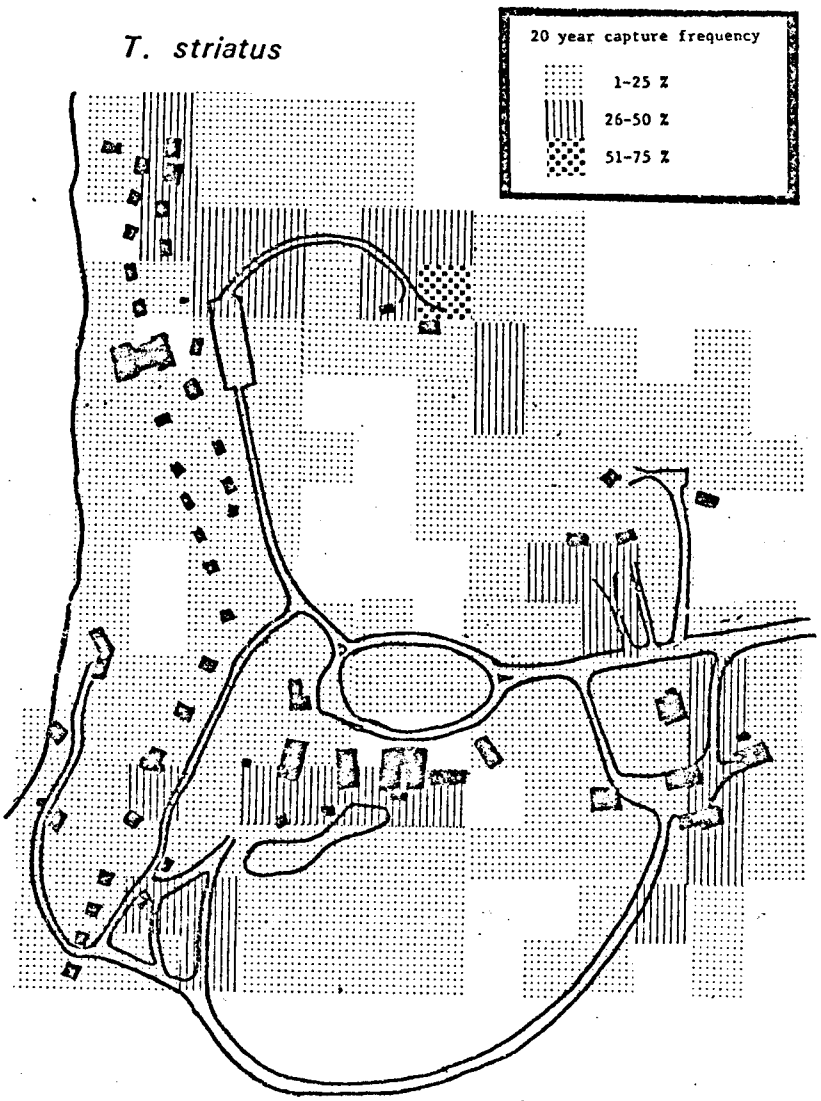


Figure 22. Frequency of at least one capture each year from 1956-1975 for Tamias striatus.

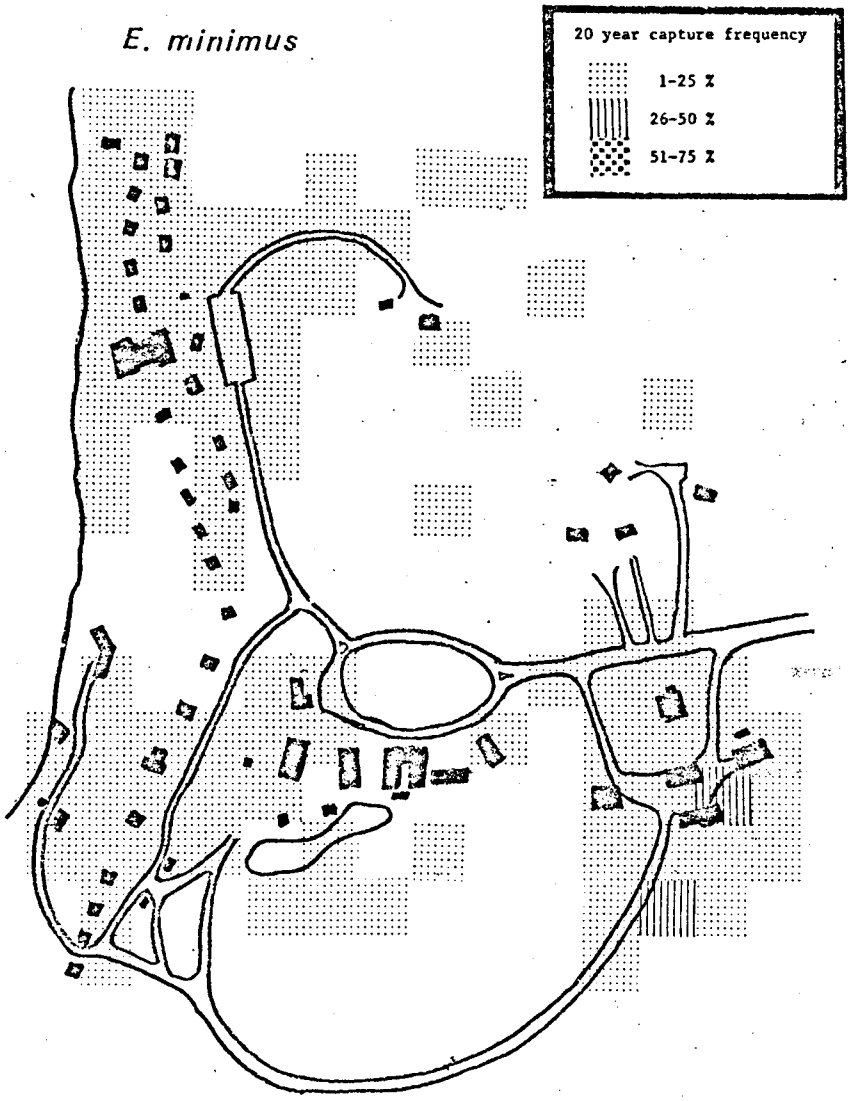


Figure 23. Frequency of at least one capture each year from 1956-1975 for Eutamias minimus.

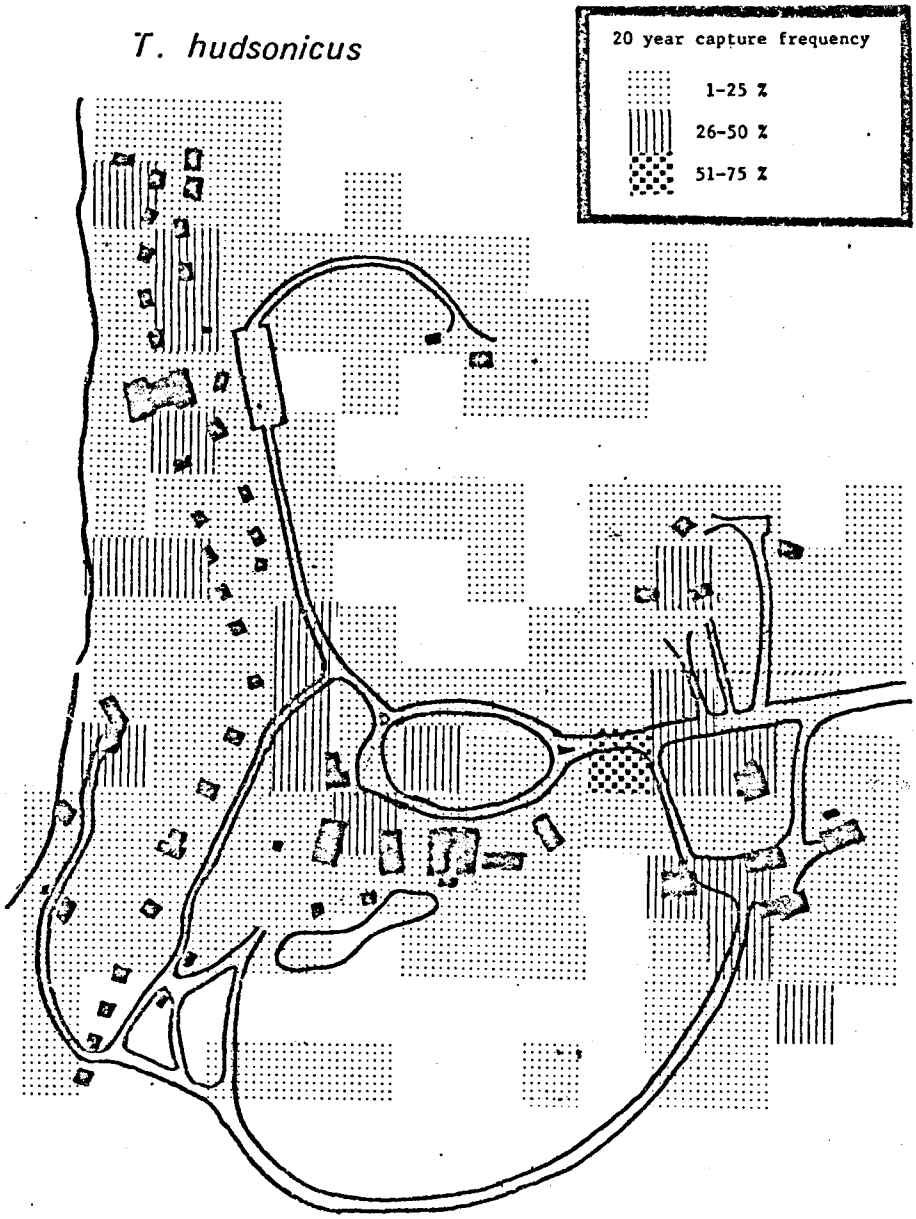


Figure 24. Frequency of at least one capture each year from 1956-1975 for Tamiasciurus hudsonicus.

DISCUSSION

The mention of 10-year cycles in animal populations immediately brings to mind the work of Keith (1963). He has recently reviewed this phenomenon (Keith, 1974) and proposes a model where the snowshoe hare (Lepus americanus) - vegetation interaction can initiate a decline phase in the hare population. This is extended by food shortage, poorer reproduction and health, and increased predation pressure. With eventual low population levels, the upswing begins until a peak is reached and the cycle can start over again.

During the low period, predators will probably encounter other prey species more often than hares. The predator will in effects be "switching" prey species, and these previously "buffered" species will then decline. Thus, other species may be tied into the cycle indirectly.

Despite the workability of this model, biological explanations of population cycles have been difficult and often incomplete (Keith, 1974; Krebs and Meyers, 1974). The problem consists of two parts. First, do we have real cycles present, and second, if we do, what is the biological interpretation? The Itasca data indicate that some of the species of sciurids may indeed have a periodic population cycle. This is probably most true for S. franklinii. Sowls (1948) noted 4-6-year cycles in this species at Delta, Manitoba and attributed such fluctuations to climatic extremes, infertility, and/or disease. He also felt S. franklinii was not an important prey species. This seems hard to believe since these ground squirrels are gregarious to some extent,

creating a clumped food source; they weigh close to 400 grams as adults, making them a substantial meal for most predators; and they do not have exceptionally quick responses in relation to the other sciurid species (Haggerty, 1968).

One possible explanation for the cyclic pattern could be that S. franklinii is subject to the hypothesis outlined by Keith (1974). They may have predatory "buffering" by other prey species (i.e. snowshoe hare, ruffed grouse), and when these are in low supply, the predators may turn toward S. franklinii for alternative food resources. Thus, these ground squirrels would be tied into the cycle and would show periodic declines, as indicated by the trapping data (Figure 6).

But such a postulate needs more factual substance. A ten-year cycle is not easy to document on data from 23 years. More than two cycles should be present to confirm the periodicity. Hence, one should view the results of the cycle analysis (Table I and Figure 10) with caution. Whether this species is linked into the ten-year cycle with snowshoe hare, grouse and perhaps other prey species is still open to question.

One of the initial questions in the study was to determine the factors responsible for fluctuations in population numbers. Lidicker (1973) and Krebs and Meyers (1974) have stated that multiple factors influence the dynamics of nearly all populations. Such a statement is logical but represents a momentous problem for the ecologist to validate by testing. The analysis used here was designed to show correlations, but not causations. The value of such analysis is to identify those factors which may be significantly

influential in controlling the populations. These can then be subject to testing for verification. This correlation technique has been used by numerous authors (Francis, 1970; Kemp and Keith, 1970; Meslow and Keith, 1971; Reynolds and Turkowski, 1972; Smith et al., 1974) in wildlife ecology.

The tabulated results of the stepwise regressions (Tables IX and X) are inconclusive and general conclusions cannot be made. For both regressions, the division into female and male classes was done to test the sensitivity of the analysis. If the population variation of each sex class was being accounted for by different factors, then the regression was felt to be somewhat biologically invalid. If the same independent variables were regressed for the males, females, and total adults, then the correlation was felt to have more basis. Only the variables that contributed at least 0.10 to the r^2 value were listed. The variables that had a significant F value at the step of incorporation in the regression are marked by an asterisk. These variables are the ones of interest and are statistically the more valuable in the regression.

In the first stepwise regression, the total adult capture was the dependent variable (Table IX). S. tridecemlineatus had a mixture of variables regressed to its population numbers, and they did not appear realistic. The analysis for S. franklinii is probably the most meaningful of the five species, with one variable (#23-corn growing degree days) being primary and significant for all three classes. Thus, good conditions for plant (corn) growth will be reflected in the S. franklinii population. This assumes that the natural vegetation responds to weather factors in a similar

manner as corn.

T. striatus also had a primary and significant variable (#28-continuous days below 0° F.), but its interpretation is unclear. Long runs of below zero weather would not be expected to be beneficial, even for torpid chipmunks underground. I think the explanation lies in the increasing population trend of T. striatus and the trend for colder winters. Thus, these parameters would correlate well, but the relationship has no biological meaning.

E. minimus has an assortment of variables, much like S. tridecemlineatus. Variable #23 (corn growing degree days) shows up as a significant factor; however, the low sample size for this species does not make the regression very reliable.

T. hudsonicus has an interesting set of two variables. They are both significant in all three cases and together account for 68 percent of the population variation. Variable #22 (growing season precipitation) has a positive correlation and this seems logical, since plants respond favorably to precipitation. This should favor higher red squirrel populations. The other variable (#30-winter index) is negatively correlated. In essence, the analysis indicates that warm wet winters are worse for red squirrels than cold dry winters. Since this species is active year round, the relationship does not seem meaningful. I would expect the milder winter to have a beneficial effect.

Thus, this analysis did not provide key factors that might be responsible for population changes in all the sciurid species. The difference in significance of the various factors among species is troubling. One would assume that some factor or set of factors

would have broad influence.

Because the number of individuals may be too crude a measurement for this analysis, a second stepwise regression was run with average adult weight as the dependent variable. It was felt that poor habitat conditions may result in loss of weight before the loss of an individual. The results (Table X) were no more conclusive than the first regression. The "r^2" values were a little higher, but the total number of significant variables remained about the same.

From the standpoint of this analysis, the most interesting species was T. hudsonicus. The winter index (#30) was now positively correlated. This could be interpreted as follows: in cold winters red squirrels require more metabolic heat and, as a result of fat utilization, are lighter in the spring. The only significant variable, however, was #17 (last frost date). This would indicate that late frosts are not beneficial to red squirrels. Nixon and McClain (1969) have shown this for Sciurus niger and S. carolinesis.

Generally, the stepwise regressions did not identify key climatic factors that could explain the population fluctuations of these species. One reason may be that the dependent variable was not appropriate. I would have liked to have used reproductive output, had the data been available.

Of course, the list of independent variables is almost infinite, and one has to select the few that are felt to be most appropriate for the known biology of the species. It should also be mentioned that factors other than climatic ones may be very important.

Variable #32 (intraspecific population level) was the only non-climatic factor tested. It was significant in the weight analysis for S. franklinii.

The realms of interspecific competition and predation were not studied. Initially, all populations were correlated in a one to one matrix. None of the populations had high positive or negative interspecific correlations. It was felt that a sensitive measurement for competition could not be extracted from the data base. Information on predation was only anecdotal. These may well be the factors which have a major influence on the population dynamics of these sciurids.

The basic pattern of survival seen in Figures 11 through 15, is type II (Deevy, 1947), which means constant mortality per age class. Closer inspection of either the tabulated data (q_x) or the survival curves (Figures 11-15) reveals that the type II diagonal line is not straight but has steeper slopes at the beginning and end. This is interpreted to indicate increased mortality rates for juveniles and older individuals. Such a pattern is commonly found among mammals (Caughly, 1966).

Differential mortality by sex may be the outcome of mating systems and the resultant strategy of each individual. Trivers (1972) indicates that each sex may not be expected to have similar strategies. Males, for example, may suffer higher mortality rates in an effort to achieve copulations with a number of different females. The risk, of course, must be outweighed by chance of high reproductive success.

Before any biological significance can be attached to the

survival curves, several points must be emphasized. First, the data are calculated in such a manner as to indicate minimal survival; that is, disappearance due to death or emmigration. This makes the survival curves more conservative than might be the case. Second, animals sampled were most likely not all residents of the Itasca Station area with established home ranges. "Drifters" or "floaters" would also tend to make the survival curve conservative. Third, the life tables these curves are based upon are a dynamic-composite type. In combining all juveniles into one cohort, one has to assume a stationary age distribution. This is probably not true for these populations. Despite these factors, similar survival curves have been generated for these same species from other studies (McCarley, 1966; Davis and Sealander, 1971; Tyron and Snyder, 1973; and Murie, 1973).

S. tridecemlineatus females had a slightly better survival than males (Table III and Figure 11). McCarley (1966) in Texas and Rongstad (1965) in Wisconsin also demonstrated higher female survival.

S. franklinii survival curves deviate slightly from the type II diagonal, but the sample size may be the cause. Females have a higher survival, especially after the first year. Males three years of age and older were not trapped and the few data points yielded a straight line (Figure 12). Murie (1973) found a slightly greater female survivorship in Alberta. He stated that equivalent survivorship and sex ratio were unusual for sciurids.

The highest survival was found among T. striatus (Table V). Here both males and females had life expectancies over one year

(males 1.09 years, females 1.21 years). In New England, Tyron and Snyder (1973) found very high survival for this species. Combined life expectancy was 1.3 years and males had a greater survival than females (70% and 65% respectively). They remarked that this is high for a squirrel species.

E. minimus had the most aberrant survival curve and also the fewest individuals sampled. The literature does not have other population data on this species for comparison, and interpretation is thus difficult. Females do exhibit greater life expectancy.

Red squirrels, T. hudsonicus, demonstrate the typical sciurid pattern of greater female longevity. The males suffer a much greater juvenile mortality. A similar curve was generaged by Davis and Sealander (1971) for red squirrels in Saskatchewan.

In the comparative summary of species survival (Figure 16), each curve is a combination of both males and females. They are plotted as a function of their percent deviation from the mean length of life to enable one to look at species of different longevities. The pattern of survival between these five species is very similar.

Life expectancy comparisons (Figure 17) demonstrate the different "e_x" values for females and males. These summarize the above discussion on survival. For S. tridecemlineatus, T. striatus, and T. hudsonicus life expectancy is short for juevniles and old individuals. Females have greater life expectancies than males. Data for S. franklinii and E. minimus may not show these patterns because of the small sample size.

According to Trivers (1972), a juvenile sex composition of

50% males would be expected. The values in Table II do not differ statistically from a 50:50 ratio for S. tridecemlineatus and S. franklinii juveniles. McCarley (1966), Rongstad (1965), and Murie (1973) found similar ratios in their juvenile populations.

A higher proportion of juvenile males than expected was found for T. striatus, E. minimus, and T. hudsonicus at the Itasca Station. This is not supported by the literature, where 50:50 ratios are reported (Kemp and Keith, 1970; Davis and Sealander, 1971; Tyron and Snyder, 1973; and Pidduck and Falls, 1973).

For adults, only S. franklinii and T. hudsonicus had 50:50 sex ratios. Kemp and Keith (1970), Davis and Sealander (1971), Iverson and Turner (1972), and Murie (1973) all report similar ratios. The other three species had fewer adult males than females. With S. tridecemlineatus, male composition was 39 percent at Itasca, 31 percent in Texas (McCarley, 1966), and 38 percent in Wisconsin (Rongstad, 1965). Trivers (1972) points out that deviations in the adult sex ratio are probably very common and reflect the differential mortality of the sexes. This would indicate that male S. tridecemlineatus suffer greater mortality as adults. Both Rongstad (1965) and McCarley (1966) attribute this mortality to increased predation pressure on young males because they disperse greater distances than females.

Tyron and Snyder (1973) found a statistically significant skewed ratio for T. striatus, but it was in favor of males. Their New England study had a very large sample size, but covered only a few years. Pidduck and Falls (1973) found an equal ratio in a small sample in Ontario, Canada.

The literature does not support a higher proportion of males in E. minimus. Both Forbes (1966) and Sheppard (1968) demonstrated equal ratios in their study populations. The former author sampled in the Itasca area.

Average adult weights of each of the five species (Figure 18) fall into five distinct classes. Even the long-term means with ± 1.96 standard deviations do not show overlap. Brown and Lieberman (1973) have discussed how separation by body weight can result in ecological differentiation in desert rodents. In their study, weight averages differed by a factor of 1.5 or more from the next higher class. Diamond (1973) also found a similar weight ratio among various species of fruit pigeons in New Guinea. In both these studies, weight classes were directly related to the food utilization curve of that species, i.e., larger individuals procured larger food items.

Weight ratios for my data were greater than 1.3. The two chipmunk species were 2.1 times apart in average weight and the two ground squirrel species were 2.2 times different. This separation may be the result of greater competition between closely related species. The distinct difference in weight classes cannot yet be fully explained, but I do not believe it is the sole determinant for ecological separation.

The use of different habitats in the study area, as indicated by the recapture data, appears to be the prime method of resource partitioning. Grassy areas provide habitat for S. tridecemlineatus (Burt, 1957; Hohn, 1966) but not for the other species. This gives the thirteen-lined ground squirrels a food resource not heavily

utilized by the other sciurid species. Of course, some overlap is expected, but the degree is the critical question for the species.

T. striatus and E. minimus may have more resource overlap than other pairs of sciurid species. Whether interspecific competition is important in determining the population trends of these two chipmunk species is not apparent. It is noticeable though, that T. striatus has had an increasing population over time (Figure 7) and E. minimus has generally declined over the years (Figure 8). An alternative explanation could be a change in habitat. The increase in deciduous woody plants may be more suitable for T. striatus than E. minimus. Forbes (1966) concluded these two species were ecologically quite distinct, and a major portion of the separation came from different habitat preferences.

S. franklinii is also a species that prefers the edges of wooded areas, using the herbaceous and woody understory for food and shelter (Burt, 1957; Haggerty, 1968). The recapture locations (Figure 21) bear this out for the Itasca Station population. Thus, this ground squirrel and the two chipmunk species appear to be using the same habitat. Either the resources present are not limiting to the populations, or the species are using each resource with different efficiencies. Detailed analysis of food utilization may resolve the question.

T. hudsonicus does not have an ecological "sibling" at Itasca. The other sciurid species cannot effectively utilize the cone crop of the conifers, or buds and fruits of large deciduous trees. If there is resource competition with the red squirrel, it is most likely occurring in ground foraging.

Coexistence of the sciurids at the Itasca Station would indicate habitat and resource partitioning. The ecological separation may be reflected in the widely differing weight classes, in differential food utilization, and/or in habitat preference. The exact extent of interspecific competition is not clear at this time, but is likely to be of vital importance in understanding the population dynamics of this sciurid community.

SUMMARY

For the past 23 years (1953-1975) a mark/recapture project has been conducted at the Itasca Forestry and Biological Station, Itasca State Park, Minnesota. Spermophilus tridecemlineatus, S. franklinii, Tamias striatus, Eutamias minimus, and Tamiasciurus hudsonicus are the sciurid species that have been trapped every summer. Capture records have accumulated into a data reservoir which was used to examine some aspects of the population ecology of these five species.

The changes in local population density each year may be following a cyclic pattern. S. franklinii demonstrates the strongest case for periodicity but causal mechanisms are still unclear. A predator-prey system is suggested, but further work is needed for definitive relationships.

Climatic variables influence populations, but consistent and significant factors were not found in the regression analysis. Yearly fluctuations may be a result of predation, intra- or interspecific competition.

Three juvenile and three adult sex ratios were skewed significantly from a 50:50 ratio. Supportive data from the literature for a skewed ratio were only found for S. tridecemlineatus adults. Greater dispersal distances and associated higher mortality were suggested as causing a decrease in males. S. franklinii and T. hudsonicus had equal sex ratios for adults and this was also reported by other investigators.

Average weight spans for the five sciurids do not overlap,

and this relationship was discussed in the light of interspecific competition. The biological interpretation of these differences in weight classes requires more research. Detailed food analysis might be one method which could substantiate the idea of ecological separation by weight.

In conjunction with resource partitioning, habitat differences are expected. The Itasca recapture data do show that various habitats are being preferentially used. S. tridecemlineatus is found in open grassy areas, S. franklinii is associated with "edge" habitat, T. striatus occupies the deciduous shrubs, E. minimus prefers the more open areas around buildings, and T. hudsonicus is found close to spruce and fir. These divisions are not absolute, but are consistent enough to have documentation from the literature.

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